# Chapter 18
# Making Sense of the Evidence: Synthesizing Paleoecological Data

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**Abstract** Paleontologists are increasingly concerned with understanding the biology of extinct species and their environments. This has resulted in a proliferation of new techniques and methodologies that provide a wealth of new data for understanding the paleobiology of extinct species and paleoecological relationships between them and their environment. However, combining such analyses to reconstruct an ancient terrestrial ecosystem can present many challenges, particularly when different lines of evidence appear to provide contradictory information. Here, we discuss some of the ways that taphonomy can bias primary data and how awareness of such issues can increase the accuracy of paleoecological studies. We discuss two geographically and temporally disparate fossil sites as examples of paleoecological reconstruction (the Pliocene of East Africa and the early Oligocene of central Chile) and possible ways of reconciling apparently contradictory data and analyses. We conclude that reconstructing ancient ecosystems requires: (1) accurate data and knowledge of potential biases; (2) a thorough understanding of the analytical techniques being applied and their *a priori* assumptions; and (3) a willingness to recognize non-analog species, habitats, and communities when necessary.

**Keywords** Taphonomy • Non-analog • Scale • Paleoecological reconstruction

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## Introduction

The field of paleontology has changed dramatically and rapidly over the past several decades. Although identifying species in the fossil record and determining their evolutionary relationships (systematics) is still a primary focus of paleontological studies, an increasing number of investigations now focus on understanding the biology of extinct species (paleobiology) and the biotic and abiotic contexts in which they lived (paleoecology). With this greater emphasis in paleobiological and paleoecological studies has come a proliferation of techniques (as detailed in this volume) for understanding how extinct species lived and moved, the habitats in which they lived, and the climatic regimes that affected them and their habitats. These advances have revolutionized our understanding of the paleobiology and paleoecology of past organisms (e.g., Hopley et al. 2007; Goillot et al. 2009; DeMiguel et al. 2010; papers in Harrison 2011a, b; Biasetti et al. 2012; Merceron et al. 2012) and allowed us to better document the timing and context of adaptations and evolutionary histories (e.g., Campisano and Feibel 2007; DeMiguel et al. 2010; Levin et al. 2011; Eiler et al. 2014).

While these advances in techniques and methodologies have provided us with more data than ever to reconstruct paleobiology and paleoecology, they have also introduced new challenges. Most conspicuously, different types of data and analyses can provide conflicting evidence about the habits of extinct species and the habitats in which they lived. In some instances, this can simply reflect species or habitats that have no close modern analog. In other cases, such apparently conflicting data can be reconciled through closer inspection of methodological assumptions and limitations of particular techniques. Here, we briefly discuss two key factors that should be considered when reconstructing the paleoecology of a fossil site – the reliability of the fossil record and the scale at which ecological proxies operate –

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and provide examples of how knowledge of these factors can inform and refine paleoecological studies.

## Contextual Considerations

### *Reliability of the Fossil Record*

Many factors act upon a fossil assemblage during accumulation and fossilization that can result in compositional unfaithfulness compared to the original community. It is not difficult to imagine why this would be of particular concern to those interested in paleoecological analysis; accuracy and precision in paleoecological inference are directly related to the fidelity of the fossil assemblage compared to the original community. The fossil record, by its very nature, is incomplete in terms of both the species and skeletal elements that are represented. This, in turn, impacts the types of analyses that can be conducted and the inferences that can be made. Taphonomy – the study of the processes that impact the remains of past living organisms from death through their transition into the lithosphere (Efremov 1940) – strives to understand the processes and agents at work in the past that are responsible for the species and elements preserved in a fossil assemblage. Understanding the taphonomy of a site acts like a lens by bringing the fossil assemblage into clearer focus, but this requires knowledge of several factors including the manner in which the remains accumulated and the time interval during which they became part of the fossil record (Fernández-Jalvo and Andrews 2016).

**Mode of accumulation**: The agent(s) responsible for the accumulation of a fossil assemblage can profoundly affect both species composition and element representation. Predators significantly alter these aspects by preferentially selecting certain prey and processing their remains (Brain 1980; Blumenschine 1988; Lyman 1994; Fernández-Jalvo and Andrews 2016), often resulting in a sample that is a biased subset of the species present on the landscape. For example, hyaena-ravaged samples often lack articular surfaces (Lyman 1994), and prey preference can heavily skew the species composition of raptor-generated rodent accumulations (Reed and Denys 2011). At the opposite end of the spectrum, species associations can be artificially inflated when the agent of accumulation is a river that can move remains from one region (habitat) to another. An example of such a phenomenon is the so-called bone conglomerate (conglomerado osífero) at the base of the Ituzaingó Formation in northeast Argentina (Cione et al. 2000), which preserves a wide variety of late Miocene fossil remains derived from an unknown proportion of the drainage basin of the Paraná River. Mode of accumulation can be thought of as a type of geographic sampling that either restricts or expands the area of the landscape that is actually sampled. The ideal scale of such sampling largely depends on the geographic extent of the modern faunas to which a paleofauna is being compared (Croft 2013).

**Duration of accumulation and fossilization**: As for mode of accumulation, the span of time over which an assemblage accumulates and becomes integrated into the fossil record can also affect the number of species represented. The ideal situation is a “snapshot” of an ancient ecosystem – an assemblage that was preserved quickly in a catastrophic event (e.g., Cladera et al. 2004; Tucker et al. 2014) – but such cases do not constitute the majority of terrestrial mammal sites. More commonly, bones accumulate and are fossilized over an extended period, resulting in time-averaging, a phenomenon that can inflate species richness and generate false associations among species that were separated in time by up to hundreds of thousands of years (or even more). If environmental conditions were changing during this interval and accompanied by shifts in habitats and vegetation, the implications for paleoecological reconstruction are clear: the site will not closely resemble a single modern habitat but rather a mixture of those that existed over an extended period. Such temporal “smearing” is the primary rationale for limiting an ecological diversity analysis to a relatively narrow stratigraphic interval within a thick fossiliferous geological formation (e.g., Kay and Madden 1997; Kay et al. 2012). How does one determine the duration over which a fossil assemblage accumulated? On a formation-wide scale, geochronological and sedimentological data can provide absolute ages for particular stratigraphic intervals. The degree of weathering on bones can provide clues about how long bones were accumulating prior to burial (Behrensmeyer 1975), as can breakage patterns (Behrensmeyer and Hill 1980; Lyman 1994) and the extent of root and insect damage. The time interval that must be taken into account must be extended further if bones are transported post-burial (uncovered and redeposited) through fluvial action, carnivore or rodent activities, and/or bioturbation (e.g., Voorhies 1969; Blumenschine 1988; Fernández-Jalvo and Andrews 2016).

Understanding the taphonomy of a fossil site is seldom straightforward, but clues can be gathered from both the specimens themselves as well as the species they represent. Much work has been done to better identify and understand taphonomic traces on bones, including Voorhies (1969), Behrensmeyer (1975, 1980), Behrensmeyer and Hill (1980), Blumenschine (1988), Fernández-Jalvo and Andrews (2016); the last of these references is an excellent, recent

**Table 18.1** Types of evidence relating to reconstructing paleoecology

| Evidence Type | | Temporal Scale | Spatial Scale | Paleoenvironmental Inferences |
|---|---|---|---|---|
| Paleosol | Trackways, trails, nests, burrowing | Minutes–years | 10–100 m$^2$ | Substrate type, climate |
| | Biomarkers | Lifetime of an individual | Locality | Vegetation, temperature, climate, water availability |
| | Soil/sediment | $10^3$–$10^5$ years | Locality | Vegetation, climate, water availability, geomorphology |
| Skeletal remains | Microwear | Days–weeks | Habitat of an individual | Vegetation structure |
| | Isotope | Weeks–months; lifetime of an individual | Habitat of an individual | Vegetation, water availability, climate |
| | Mesowear | Months to years | Habitat of an individual | Vegetation structure |
| | Microstructure | Lifetime of an individual | Habitat of an individual | Ecological pressures |
| | Gross (functional) Morphology | $10^5$–$10^6$ years | Habitat of an individual | Vegetation, substrate type, climate |
| Paleobotanical remains | Phytoliths | Months–years; $10^2$–$10^5$ years | Locality-region | Vegetation, climate |
| | Pollen | Months–years; $10^5$–$10^6$ years | Locality-region | Vegetation, climate |
| | Spores | Months–years; $10^5$–$10^6$ years | Locality-region | Vegetation, climate |
| | Macrobotanicals | $10^5$–$10^6$ years | Locality | Vegetation, climate |

monograph that documents these modifications in atlas form. Since these modifications result from taphonomic processes, they provide a direct way of inferring potential biases in a fossil assemblage.

Another approach to taphonomy that can be used in conjunction with direct methods are inferential ones that aim to gauge the completeness (or rather incompleteness) of a community based on its ecological attributes. Body size, as detailed by Hopkins (2018), is a critical biological constraint and one of the three key variables typically included in an ecological diversity analysis (along with diet and locomotor style; Kovarovic et al. 2018). Body size dictates metabolic and energetic limits, and deviations from the expected patterns of body size distribution (based on extant communities from different habitats) can help gauge taphonomic bias (Damuth 1982; Soligo 2001; Soligo and Andrews 2005; Fernández-Jalvo and Andrews 2016). Combining body size distributions with dietary data can permit specific taphonomic biases to be identified. For example, many Pliocene-Pleistocene African faunal communities lack small primary consumers, which is not characteristic of any modern African habitat, suggesting that these fossil assemblages are taphonomically biased against this ecotype (Soligo and Andrews 2005). Basing an ecological diversity analysis on the entire assemblage would almost certainly result in spurious paleoenvironmental and paleoecological interpretations.

All fossil assemblages are almost certainly incomplete to some degree simply due to the nature of the fossilization process. A key question, then, is how complete a fossil assemblage must be to yield reliable paleoecological information. Many studies have examined the effects of taphonomic bias on community structures, particularly as it relates to time-averaging and faunal mixing (e.g., Dreyer 1984; Foote 1992; Mares and Willig 1994; Robb 2002; Andrews 2006; Louys et al. 2009); however, much more research is necessary to better understand how taphonomic bias impacts fossil faunal community structure and ecological signal. It is not an exaggeration to say that understanding taphonomy is fundamental to understanding faunal communities and environments of the past and, by extension, evolutionary processes (Fernández-Jalvo and Andrews 2016).

## *Questions of Scale: What Are the Data Telling Us?*

The types of evidence gathered to reconstruct paleoenvironment and paleoecology reflect a wide range of temporal and spatial scales, and each can bring a different type of information to bear on environmental reconstructions. While integrating a variety of analytical approaches is essential for arriving at a complete and nuanced picture of an ancient community, it can also highlight conflicts between different lines of evidence. Such apparent conflicts are often partly due to the different temporal and spatial scales at which such analyses operate. Here, we briefly discuss the type of evidence commonly used in paleoecological analyses and the time scales they reflect (see Table 18.1).

**Trace fossils**: As Hembree (2018) describes, trace fossils are the preserved remains of behavioral interactions between an organism and a substrate (e.g., burrows, tracks, trails, nests, borings). These traces preserve an instant in time (hours to days) and have important behavioral and environmental implications.

**Skeletal elements**: Skeletal elements (including teeth) provide biological information about the individual and the species to which they belong and can provide information about body size (Hopkins 2018), functional morphology (Dunn 2018; Evans and Pineda-Munoz 2018), diet (Evans and Pineda-Munoz 2018; Green and Croft 2018; Higgins 2018), and life history (Hogg 2018), all of which can provide primary data for paleoecological reconstructions (see applications in Barr 2018; Curran 2018; Kovarovic et al. 2018; Vermillion et al. 2018). The spatial scale over which skeletal elements operate depends on the geographic range of the individual or, more commonly, on the population, since many studies based on skeletal elements pool data from multiple individuals within an assemblage. On a temporal scale, even though skeletal data derive from an individual, they can represent adaptations that evolved over millions of years (e.g., gross tooth morphology, Evans and Pineda-Munoz 2018), use over an extended portion of an individual's lifetime (e.g., mesowear, Green and Croft 2018; enamel isotopic composition, Higgins 2018), or even to short-term use (e.g., microwear, Green and Croft 2018).

**Paleobotanical remains**: Plant fossils are direct evidence of vegetation and include pollen and spores (Mander and Punyasena 2018), phytoliths (Strömberg et al. 2018), and macrobotanical remains such as fossil leaves (Peppe et al. 2018). Similar to skeletal remains, paleobotanical remains can represent varying spatial and temporal scales ranging from site-specific (phytoliths, pollen, spores, macrobotanicals) to regional or an even wider geographic area (pollen, spores). In addition to providing evidence of the vegetation present at a site, paleobotanical remains can be used to reconstruct paleoclimate and paleoenvironment, particularly if data are available from different geographic regions, basins, and stratigraphic intervals (see Mander and Punyasena 2018; Strömberg et al. 2018; Peppe et al. 2018).

**Paleosols**: Ancient soils preserve information about the climate, ecosystems, and sedimentary systems in the past. Contained within paleosols are macroscopic, micromorphological, mineralogical, and geochemical indicators of paleoenvironment that reflect the vegetation, climate, sedimentary processes, and landscape stability of a site (Beverly et al. 2018). In addition to skeletal elements and paleobotanical remains, paleosols often also preserve organic biomarkers, another useful indicator of paleoenvironmental and paleoclimatic conditions (Berke 2018). Data from paleosols are generally locality-specific, although pollen and spores can be carried over long distances by wind or water (Mander and Punyasena 2018).

None of the different types of data described above exists in isolation, and most are found together at a fossil site. The different spatial and temporal scales they represent (Table 18.1) can highlight different aspects of an ecosystem and introduce complications for arriving at an integrated understanding of the paleoecology of a fossil site. Below, we present a pair of very different case studies to illustrate the challenges and possibilities of integrating multiple datasets when reconstructing a past ecosystem.

## Case Studies

### *Laetoli, Tanzania*

Laetoli, located in northeastern Tanzania on the margin of the Eyasi Plateau, is one of the most intensively sampled and best-studied early hominin sites (see papers in Leakey and Harris 1987; Harrison 2011a, b). Fossils of *Australopithecus afarensis* have been recovered from the Pliocene Upper Laetolil Beds (ULB, 3.85–3.6 Ma) (Harrison 2011c) along with a diverse assemblage of associated fauna and flora. Laetoli is famous for preserving sets of hominin trackways along with those of other fauna (Leakey and Harris 1987; Harrison 2011a, b). Detailed studies of taphonomy and paleoecological proxies have been conducted for the site (papers in Harrison 2011a, b), the results of which are summarized and synthesized here.

**Taphonomy**: Vertebrate remains primarily consist of isolated skeletal elements, although partial skeletons of mammals <5 kg are common (Su and Harrison 2008). They are in various stages of disarticulation and weathering. Pre-fossilization damage, such as weathering, breakage, root etching, carnivore damage, rodent gnawing, insect damage, is common and indicates that many specimens were exposed on the land surface for a period of time before burial (Su and Harrison 2008). Carnivores were active agents in the accumulation of the Laetoli assemblage as evidenced by the commonness of toothmarks on fossils, high taxonomic diversity of carnivores, and abundance of carnivore coprolites (Su and Harrison 2008). There is no evidence of fluvial transport of the bones. The sedimentary setting (mostly aeolian tuffs) and bone preservation suggest that vertebrate skeletal remains were naturally scattered on successive land surfaces prior to being buried by subaerially deposited volcanic ashes (Hay 1987; Su and Harrison 2008). Thus, one can be reasonably sure that the Laetoli fossil assemblage is a good representation of the original community, although taphonomic biases against animals in the

25–50 kg weight range and micromammals (<1 kg) appear to be present (Su and Harrison 2008).

**Paleoecological proxies and indicators**: The Laetoli faunal assemblage is dominated by taxa generally associated with more open habitats (e.g., alcelaphin bovids, leporids, pedetid rodents, phasianid and numidid birds) (Su 2011). Traces of termitaries, signs of extensive termite bioturbation, burrows and nests of solitary hymenoptera, and achatinid gastropods all suggest that soils were generally dry and well drained for much of the year (Darlington 2011; Tattersfield 2011; Harrison et al. in press). The aridity of Pliocene Laetoli is also indicated by the absence of aquatic and hydrophilic vertebrates (e.g., hippopotamids, crocodylids, testidudines), which confirms that large permanent sources of water were not available on the landscape (Su and Harrison 2015). Community structure analysis indicates a fauna most similar to those from open woodland, bushland, and grassland habitats (Su 2011). Initial studies of the pollen from ULB identified herbaceous plant families common in the area today, with a high proportion of Poaceae and *Acacia* pollen, suggesting a grassland-open woodland habitat (Bonnefille and Riollet 1987). However, subsequent re-sampling of the ULB sediments recovered no palynomorphs, suggesting either poor preservation of pollen at Laetoli or modern pollen contamination in the initial study (Rossouw and Scott 2011). Phytoliths indicate that grasses were common but not dominant in the ULB; furthermore, most unclassified phytoliths pertain to trees and shrubs (Rossouw and Scott 2011). These phytolith results are supported by enamel isotopic and mesowear studies indicating that mixed-feeders dominate the ungulate fauna (Kingston and Harrison 2007; Kaiser 2011; Kingston 2011). Ecomorphological analyses of bovid postcranial remains suggest that most specimens reflect heavy or open woodland habitats (Kovarovic and Andrews 2007, 2011; Bishop et al. 2011). The terrestrial gastropod community is closely associated with woodland and forest vegetation today (Tattersfield 2011), and the primates, which include arboreal and semi-terrestrial taxa, would have required dense woodland (Harrison 2011d). Plant macrofossils consist of wood, root casts, leaf impressions, fruits and seeds from taxa found in forest and dry open woodlands (Bamford 2011a, b). A sedge rhizome with basal culms is the only element recovered commonly associated with water-margin environments.

**Synthesis**: The paleoecological indicators and proxies from Laetoli appear to present disparate strands of conflicting evidence, with certain proxies signaling arid, open conditions and others suggesting more mesic and wooded conditions. While the large mammal community is dominated by taxa generally associated with dry, open habitats, enamel isotopic and mesowear analyses suggest that these taxa were not as specialized in their dietary preferences in the Pliocene as their extant relatives are today and that substantial C3 resources (i.e., trees and shrubs) must have been available on the paleolandscape. Ecomorphological studies of bovids indicate that most of the specimens sampled represent species that were forest or heavy-cover adapted. Postcranial elements of dik-dik (*Madoqua*, the most common bovid at Laetoli) make up a substantial proportion of the sample, a finding that has the potential to skew interpretations; although extant *Madoqua* species inhabit dense thickets and bushes, they do so in more open habitats. The terrestrial gastropod community appears to provide more accurate information about microhabitats within the Laetoli area than large mammals, as they vary over relatively small spatial scales in relation to fine-grained ecological differences. These gastropod communities suggest that dense woodland vegetation was scattered across the Pliocene Laetoli landscape, possibly along seasonal river courses (see below).

The faunal and floral evidence suggest that the vegetation of Pliocene Laetoli included a complex mosaic of woodland, bushland, shrubland, grassland with riverine woodland in a relatively arid and seasonal environment. Sedimentological studies indicate that water-worked tuffs are a relatively minor component of the sedimentary sequence. A small proportion of these tuffs were deposited in shallow bodies of standing water, likely ephemeral ponds that dried up during the dry season (Ditchfield and Harrison 2011; Harrison and Kweka 2011). Most of the water-worked tuffs are fluvially reworked and found in minor channel fill sequences at several localities, suggesting a well-developed and relatively sizable seasonal local drainage system that flowed in the wet season (Ditchfield and Harrison 2011). In present-day Laetoli, water run-off from the volcanic highlands flows below the surface year-round, and the water emerges as permanent springs along the margin of the Eyasi Plateau escarpment where the sediments interface with the underlying impervious Precambrian basement rocks (Harrison 2011d). Given that similar geomorphological and topographic features were already in place in the Pliocene, it is likely that small, perennial springs were present in the Laetoli area. The Pliocene hydrological system described here would have been able to support the complex mosaic of vegetation suggested by the faunal and floral evidence.

Except in rare cases of mass death events, fossil assemblages are almost always time-averaged. The Laetoli fossil assemblage samples a 200–300-ky interval. How do we know that the hominins in this assemblage were living in the same environment as the fauna with which they are associated? Serendipitously, trackways of mammals and birds, along with those of hominins, were preserved in thin layers of ash, each of which was probably produced by successive eruptions over the course of a few weeks (Hay 1987). Most of the footprint layers show little lateral change in thickness; this observation, combined with the excellent preservation of the footprints, suggests that the layers were essentially undisturbed after deposition and quickly buried (Hay 1987). The remarkable preservation of raindrop imprints on these ash layers suggests that they were laid down during the transition from the dry to rainy season (Hay 1987). The trackways preserve prints of many taxa represented by skeletal assemblage and their abundances are similar to those of the skeletal assemblage (Leakey 1987). For example, *Serengetilagus* (hare) and *Madoqua* (dik-dik) are the most common taxa in the skeletal assemblage, and their prints are the most numerous in the trackways (Leakey 1987). These trackways represent what is essentially a single point in time. In combination with detailed analyses of changes in taxonomic composition (fauna and phytoliths) and community structure over time, they tell us that the paleoenvironment during Pliocene Laetoli was remarkably stable throughout the 200–300-ky interval (Su and Harrison 2007).

## *Tinguiririca (Termas del Flaco), Central Chile*

The fossil site known as Tinguiririca is located in the eastern end of the Tinguiririca River valley in central Chile near the tourist town of Termas del Flaco, roughly 150 km south-southeast of the Chilean capital of Santiago. The fossils derive from the Abanico Formation (Charrier et al. 1996; Wyss et al. 1993, 1994) and pertain to the early Oligocene (33–31 Ma) based on high-precision $^{40}Ar/^{39}Ar$ radiometric dates within and below the fossil-bearing horizon and biostratigraphic correlation with other dated faunas from southern Argentina (Flynn et al. 2003; Croft et al. 2008). Twenty-six species of mammals have been identified at the site (Croft 2016: Appendix 7), most of which (80%) belong to extinct orders endemic to South America.

**Taphonomy**: Fossil preservation in the volcaniclastic Abanico Formation (including Tinguiririca) contrasts with that of most fossil sites. The sediments represent volcanic mudflows (lahars), and preserved specimens appear to represent elements that were on the landscape when the lahar took place (bone fragments) as well as living animals that fell victim to the flow (complete skulls and articulated elements). Preservation is generally excellent, though removing the extremely hard sediment is both challenging and time-consuming; consequently, only a subset of recovered specimens have been cleaned and identified, mainly those that preserve teeth. No animals other than mammals have yet been identified at Tinguiririca, but this may partly be due to preferential preparation of craniodental specimens; it is possible that postcranial bones of birds or other vertebrates remain encased in sediment. Since lahars are geologically instantaneous events, the fauna is thought to represent a very short temporal interval, an inference supported by the tight clustering of dates directly associated with the fauna (Flynn et al. 2003). The specimens derive from a small geographic area (<10 km$^2$), but it is not known how far the bones may have been transported prior to burial. Therefore, the full extent of the area sampled cannot be determined. The fauna is biased against small mammals (<800 g), which represent roughly 25% of the fauna (Croft et al. 2008).

**Paleoecological proxies and indicators**: The unusual preservation conditions at Tinguiririca preclude many types of paleoecological analysis; no paleosols are present, no ichnofossils have been identified, and botanical remains of all types are also lacking. Thus, the mammal fauna has provided the only means of inferring the site's paleoenvironment. Several lines of evidence, including faunal hypsodonty, body size distribution (cenogram) analysis, and ecological diversity (community structure) analysis suggest that the mammals of Tinguiririca inhabited a dry, relatively open landscape with few trees and abundant low, herbaceous vegetation (Croft 2001; Flynn et al. 2003; Croft et al. 2008).

**Synthesis**: A peculiar aspect of the fossil record of South America that has long been recognized is that hypsodont mammals – those with high-crowned cheek teeth – appear 10–15 million years earlier than on other continents (e.g., Scott 1937; Patterson and Pascual 1968). This "precocious hypsodonty" has generally been thought to correlate with the early appearance of grasses and open habitats in South America (Webb 1978; Stebbins 1981), and Tinguiririca has figured prominently in these discussions because it represents the earliest interval in which hypsodont mammals predominate (Wyss et al. 1994; Flynn et al. 2003; Croft et al. 2008). The paleoecological analyses of Flynn et al. (2003) provided additional support for the early appearance of open habitats in South America, but considering that most (nearly 90%) of Tinguiririca species lack close living relatives and/or clear ecological analogs, one might rightly question whether its paleoenvironment can be accurately reconstructed based on the presumed paleoecological attributes of its mammals. Indeed, concern about a potential lack of correlation between hypsodonty and open-habitat feeding in notoungulates, the predominant herbivores at Tinguiririca, prompted Croft et al. (2008) to exclude browsing, mixed feeding, and grazing categories from their ecological diversity analysis and conservatively code all non-frugivorous herbivores as folivores. Like the study of Flynn et al. (2003), that of Croft et al. (2008) concluded that Tinguiririca most likely represented an open habitat, but it also highlighted the fact that the Tinguiririca mammal community had an ecological structure quite unlike any modern South American community. Such "non-analog" mammal associations have long been documented at Pleistocene sites in North America (see Semken et al. 2010 and references therein), and it seems likely that many more examples will be documented as paleoecological analyses are applied to older intervals and other regions of the world. However, documenting such cases becomes increasingly challenging in deep time; as the evolutionary distance between fossil and modern species increases, so does the uncertainty associated with paleobiological reconstructions. As a consequence, it can be difficult to distinguish truly non-analog communities from those that appear to be non-analog due to inaccurate paleobiological reconstructions.

Although additional lines of paleoenvironmental evidence are lacking at Tinguiririca, fossil mammals of equivalent age are known from more traditional sedimentary settings about 1,000–1,500 km to the southeast in Patagonia, Argentina. Paleoenvironmental interpretations for these sites based on ichnofossil and paleobotanical evidence have varied considerably, with ichnofossil data suggesting that relatively open habitats were present as early as the late middle Eocene (Bellosi et al. 2010; Sánchez et al. 2010) and pollen and phytolith analyses indicating that such habitats did not appear until well into the Miocene (Palazzesi and Barreda 2012; Strömberg et al. 2013). However, it is important to point out that these latter studies were based on the assumption that abundant grasses – which were not present in Patagonia during the Eocene or Oligocene – are necessary for the existence of open habitats. A recent study demonstrated this assumption to be false by using the ecomorphology of phytoliths to interpret vegetation structure rather than taxonomic composition (Dunn et al. 2015); this innovative new technique, known as Leaf Area Index (LAI) analysis, concluded that late Eocene and early Oligocene habitats in Patagonia were dry to arid and had an open vegetational structure most similar to modern deserts and shrublands (Dunn et al. 2015). Mean annual precipitation (MAP) estimates for this interval (270–770 mm) based on stable carbon isotope data from mammal teeth (Kohn et al. 2015) are concordant with this interpretation. In fact, that study's MAP estimate for the Tinguirirican temporal interval of Patagonia (400 ± 160 mm) is remarkably similar to that of Tinguiririca itself (600 ± 500 mm) based on an ecological diversity analysis of the mammals of Tinguiririca, Chile (Flynn et al. 2003).

## Concluding Remarks

Reconstructing the paleoecology of a fossil site optimally draws on multiple lines of evidence, but care must be taken at all steps of the process in order to reach an accurate interpretation. Fundamentally, the data upon which any analysis is based must be sound. Understanding the taphonomy of a site is essential for understanding possible biases in data (both temporal and geographic) and a necessary first step toward dealing with such biases. Integrating the interpretations of multiple types of analyses requires knowledge of the varying temporal, geographic, and/or other scales that each samples. Apparently contradictory results can often be reconciled by carefully examining the assumptions and biases that underlie each analytical approach. Finally, *a priori* assumptions must be critically examined when reaching a final interpretation; precise and accurate data and analyses are of little use when constrained to fit within pre-conceived notions about a site or its flora or fauna. Cenozoic terrestrial ecosystems are filled with examples of non-analog plant and animal communities that can only be recognized as such when investigators are open to acknowledging their existence.

The ultimate goal of paleoecology is to aggregate detailed reconstructions of many paleontological sites over broad geographic and temporal scales in order to understand macroevolutionary events. Only by documenting variation in depositional context, taphonomy, paleobiology, and paleoecology of faunal communities through time and space can we fully answer questions about origination, extinction, and adaptation.

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